Function and Distribution of Separating Interventions in a Captive Group of Bonobos

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Abstract

The most widely discussed bonobo (*Pan paniscus*) social relationship is the intra-sexual female bond but there is mounting evidence that the inter-sexual bond may be of equal importance to the structure of the bonobo social system. Unrelated males and females form close associations and these associations are beneficial to male reproductive success. Male bonobos compete for these reproductively valuable bonds by engaging in rank struggles and by forming close associations with females. Separating interventions performed by individuals function to thwart bond formation in competitors. This behavior can be an important mechanism in determining the nature and relative importance of social relationships. The present study investigates the function and distribution of separating interventions in a captive group of 14 bonobos. Results indicate a differential distribution of both type of dyad separated, as well as performance of separating behaviors. The data presented strongly suggest that separating interventions are employed, primarily by adult males, as a counter-strategy to the establishment of their closest rivals' inter-sexual bonds, and, as an alternate mechanism to agonistic conflicts in the establishment of a dominance hierarchy.

Introduction

Ecological variables have and continue to shape the social systems of animals, including primates (Wrangham, 1987). Diurnal primates are thought to live in groups primarily because of the benefit of reduced predation risk (van Schaik, 1983). While predation is certainly a driving evolutionary force, there are costs associated with group living, namely increased travel time and competition for resources such as food and mates (van Schaik and van Hooff, 1983), which influence the disposition of conspecific relationships.

The reproductively salient resources utilized by males and females to maximize their fitness are fundamentally different and are paramount to understanding the nature of intra- and intersexual competition. Females are reproductively constrained by the quality and spatio-temporal distribution of food (Trivers, 1972; Wrangham, 1980). In some species of primates, females bond together to defend food resources from extra-group competitors (Wrangham, 1980) while others, such as chimpanzees (*Pan troglodytes*), engage in intra-group competition over valuable fruit-rich core areas (Pusey, et. al., 2008). Consequently, group size in primates is determined by the degree of female cohesion required to best maximize food resources (Wrangham, 1980). Conversely, male reproductive success is limited by the grouping pattern of, and ability to monopolize, females (Clutton-Brock and Harvey, 1977; van Schaik and van Hooff, 1983). Thus, males compete, sometimes intensely and aggressively, for access to females.

One outcome of such competition is the evolution and development of social dominance hierarchies. In many primate species, dominance rank can have a varying effect on reproductive success and, if the behavioral traits exhibited by dominant individuals lead to higher rank and are heritable, selection should favor individuals that perform them (Silk, 1987). Individuals attain

dominance rank primarily through one of three different mechanisms. First, rank may be inherited, such as in some species of matrifocal dominant macaques (Chapais, 2001). Second, individuals may participate in agonistic dominance interactions where fighting ability, age, and size are the primary determinants of rank (Clutton-Brock and Albon, 1979; and Maynard-Smith, 1982) and third, individuals may practice political maneuvers to acquire and maintain rank. A classic example of the latter is when two males join together to defeat and outrank a third male. This behavior is typically expressed as male-male coalitionary aggression in despotic species such as bottlenose dolphins (*Tursiops truncates*) (Connor et. al., 1992), olive baboons *(Papio anubis*) (Packer, 1977), capuchin monkeys (*Cebus capucinus*) (Perry, 2003) and, most copiously, in chimpanzees (deWaal, 1982 and Watts, 2002). Because this behavior occurs in a small but ecologically diverse range of species, political maneuvering behavior must have plasticity in its application in order for it to be functional. We now pose the questions: how flexible is the behavior and what if mechanisms of political maneuvering are not limited to males or focused solely on aggressive interactions?

Bonobos (*Pan paniscus*) are ideal candidates with which to look for alternate political strategies because they share a long evolutionary history with chimpanzees, the quintessential non-human political actor, having only recently diverged from a common ancestor about 2 million years ago (Doran, 2002). Bonobos are patchily distributed throughout the Democratic Republic of Congo and are geographically isolated from chimpanzee populations by the Congo River. Despite this separation, bonobos have retained many characteristics similar to chimpanzees such as body size and degree of sexual dimorphism (Parish, 1996), male philopatry (Gerloff, et. al., 1999), and female sexual swelling and ovulation timing (Stanford, 1998). Even so, field research on bonobos has revealed marked differences in behavior from chimpanzees

including: greater group cohesion (White, 1996); increased female-female and male-female association (White, 1996; Vervaecke, 2000); reduced male-male bonding and coalition formation and less intense inter- and intra-group agonistic interactions (Furuichi and Ihobe, 1994). Because of the socio-behavioral differences in *Pan*, predictions about political maneuvering in bonobos must be considered in light of grouping patterns and dominance interactions.

Grouping patterns and Dominance in Bonobos

Bonobos and chimpanzees both exhibit a fission-fusion foraging strategy to maximize fruit consumption, particularly in times of food shortage, however the habitat of bonobos yields a less variable distribution of food during particular seasons than chimpanzee habitat and is arguably the main factor contributing to the observed increased group cohesion in bonobos relative to chimpanzees (White, 1996). A cohesive grouping pattern has been shown to be a *theoretically* substantial evolutionary force driving such behavioral factors as increased female-female bonding, female coalitionary defense of food, and increased female dominance over males (Hemelrijk, 2002). Observations of both wild (Kano, 1992) and captive (Parish, 1996; Vervaecke, 2000) bonobos have shown these traits to be characteristic of bonobo sociality. Nevertheless, the degree of female dominance within bonobo sociality and where bonobos fall on the Vehrencamp's (1983) despotic-egalitarian political continuum continues to be debated (Kano, 1992; Parish, 1996; Furuichi, 1997; Stanford, 1998; Boehm, 1999; Hohmann & Fruth 2002; and White, 2007).

Some authors suggest that females have partial to full dominance over males; others contend that dominance is context dependant with males exhibiting deference only in certain

situations. White, et. al., (2007) have argued that in the context of feeding, female bonobos experience priority via male deference. According to this scenario, males allow females to feed first, resulting in increased female reproductive success from (the assumed) increased caloric intake. Female chimpanzees, in contrast, do not have feeding priority and are subordinate to all males in the group (Pusey, 1990). This key difference, combined with a greater degree of seasonal variability in fruit availability in chimpanzees, results in greater female fissioning to meet foraging needs consequently, female chimpanzees often travel alone (Pusey, 2008). In order for male chimpanzees to maximize their reproductive success, they employ political maneuvers such as male-male coalitions against other males to monopolize access to several estrous females (Gilby and Wrangham, 2008).

Unlike male chimpanzees, male bonobos do not cooperate to defend access to the core area of more than one female since the core areas of female bonobos are larger and more overlapping relative to chimpanzees (White, 1996). Instead, *male* bonobos fission and monopolize a small foraging group of females by excluding other males (White, 1996). Support for this argument comes from study in the Democratic Republic of Congo's Lomako forest where the most common bonobo party composition was found to be a single male traveling with a small number of females (White, 1996). Therefore, because of increased male fissioning, a (disputed) decrease in male dominance, and because of the importance of male-female relationships to mating success, it is unlikely that male bonobos would utilize the same male-centric political strategies as their patriarchic chimpanzee counterparts.

Political maneuvers in bonobos and other species

Given the ongoing debate about the nature of bonobo dominance, investigations into political maneuvering mechanisms can shed light on the emerging picture of the bonobo social system. Observations of other species that engage in political maneuvering have revealed little deviation from the classic male-male coalition with aggression and full male dominance template, nor has there been significant variation found with regard to sex differences in performance. Olive baboons and capuchin monkeys live in multi-male-multi-female groups with agonistic dominance hierarchies and male-male coalitions, but there have been no reports of long lasting male-male associations in these primates (Packer, 1977; Perry, 2003). In contrast, both dolphins and chimpanzees have been categorized as having a fission-fusion grouping pattern where party composition changes several times a day, yet the males of these species may form coalitions with other males and long lasting associations have been observed between males (Nishida, 1968; Connor, et. al., 2000; Watts, 2002). This evidence suggests that the male-male relationship is the most important association to the males of the species. Conversely, male-female relationships in these species are largely restricted to and contingent upon individual female reproductive states (Connor, et. al., 2000, Wrangham, 2002) rather than increased group cohesion as seen in bonobos (White, 1996). Despite the differences in grouping patterns of the species described above, males in all four of the species easily dominate females and utilize aggressive coalitions formed through male-male associations to dominate and, in some instances, eliminate (de Waal, 1982) rival males.

Although chimpanzees have shown some variation in coalition composition with instances of females supporting males in rank efforts (de Waal, 1982 and Boehm, 1999), in

bonobos it may be coalitionary support by females that is crucial to male rank maintenance and acquisition (Kano, 1992; Gerloff et. al., 1999; Hohmann, 1999). Although male-male coalitions have been observed in bonobos, there is no evidence they are utilized in male rank endeavors (Gerloff et. al., 1999), marking a major difference in the political nature of the two *Pan* species. The employment of females as coalition partners is likely because females *can* dominate males and because aggression in bonobos is less severe than in chimpanzees, thus permitting females to be just as, or perhaps more, effective coalition partners (Hohmann, 1999).

In addition to using male-male coalitions, male chimpanzees and capuchin monkeys employ another political maneuver termed 'separating interventions,' where a male intervenes into the affiliative dyads of rival males, effectively terminating the interaction (de Waal, 1982; Nishida, 1996; Perry, 2003). This behavior functions as a counter tactic to the establishment of the male-male bond necessary for coalition formation. The separating intervention behavior documented by de Waal (1982) in chimpanzees took these basic forms: 1) display behavior from a third individual directed at one or both dyad participants, 2) attack on one or both individuals, and 3) interposition between and/or displacement of individuals engaged in an affiliative dyad. [A similar behavior has been observed in savannah baboons (*Papio cynocephalus*), where females acquire male 'friends' with whom they closely associate primarily as an anti-infanticide strategy. Males often have more than one female friend leading to female competition for access and resulting in dominant female displacement of subordinates in proximity of the male friend (Palombit et. al., 1997).]

The proximate function of separating interventions is the termination of the affiliative dyad but the ultimate benefit is best explained by discussing the interchange of affiliative behavior (such as grooming) with support behavior during agonistic conflicts in species that

engage in political maneuvering. Interchange is defined as the reciprocal exchange of different social acts (Hemelrijk, 1990) and in chimpanzees, males compete for valuable coalition partners and grooming is used to form and solidify alliances (see Watts, 2002 for review). Evidence of interchange is scarce, likely because of the complexity of a task requiring some kind of cognitive book-keeping (Watts, 2002), but observations have been reported in both chimpanzees (Watts, 2002) and bonobos (Vervaecke et. al., 2000 – although results were possibly confounded by rank effects). In chimpanzees and capuchin monkeys, individuals that impose on the formation of the social bonds of competitors can impede the formation of coalitions and alliances that may be used to dominate them in the future. Thus, separating interventions can be an effective counter-strategy to the political maneuvers of rivals and are a valuable instrument in determining the relative importance of inter-group relationships in dominance rank and mating success.

Because of the association differences observed between chimpanzees and bonobos, examination of separating interventions in this species can help further determine the nature of *paniscus* political struggles and the importance of same and mixed sex social bonds associated with rank acquisition and mating success in a species whose social system continues to elude definition. This paper investigates the distribution of separating interventions in a captive group of bonobos by testing the following hypotheses.

Predictions

Dominance relations in the present study should reflect those recorded in other captive populations and I predict:

- Evidence of a linear hierarchy in both males and females with some overlap in dominance between the sexes.

Association patterns should reflect those observed in wild populations, therefore I predict:

- Greater male-female and female-female association than male-male association, in contrast to greater male-male than both male-female and female-female association observed in chimpanzees.

Because of the importance of the male-female bond to male reproductive success, I predict:

- Males will preferentially associate with females more than with males.

Given that access to females is limited and positively correlated with rank, I predict:

- High ranking males will associate more frequently with females than will low ranking males.

Because close intersexual association can forecast copulation frequency, I predict:

- Males will compete for these reproductively valuable relationships performing separating interventions into affiliative male-female dyads to hinder the formation of rival males' bonds.

Separating interventions function to thwart bonding in competitors, therefore I predict:

- Interventions will be directed at individuals closest in rank, as game theory predicts (Maynard-Smith, 1982).

Methods

Study Group

All data were collected on a captive group of bonobos housed at the Columbus Zoo and Aquarium in Columbus, Ohio. The group was composed of five adult males, four adult females, two juvenile males, two juvenile females, and two infants (one born during the course of the study and not included in the data set) (see Table 1). The animals were housed in two large indoor viewing exhibits (590 sq. ft. each) with multiple climbing structures, two off exhibit indoor enclosures (243 sq. ft. each), two off exhibit outdoor enclosures (200 sq. ft. each) and a large naturalistic outdoor exhibit (190 ft by 150 ft, 28,500 sq. ft.) with grass, trees, and an artificial stream and waterfall. The animals were fed an abundant amount each morning and evening at approximately 800 and 1730 hours. Additional feedings were sometimes given throughout the day.

Data Collection

Observational data were collected between August – November 2008 resulting in 236 hours of observation, between 900 and 1600 hours in 3 hour blocks each weekday, and rarely overlapped with feeding times. Ten minute focal samples were collected (Altmann 1974) on each individual in the study group (with the exception of the infant born after data collection began). A random list of animals was generated at the start of each data collection session, individuals were

sampled once before starting over and the preceding subject was never the nearest neighbor to the following subject. During sampling periods, all social behaviors (see Appendix A) of the focal individual (actor) and target (recipient), individual(s) within 2 m of the subject, were recorded.

Participants in all affiliative dyads in the group were identified at the top of each focal minute. Affiliative dyads were defined as any episode where two individuals were engaged in affiliative (see appendix A for list of affiliative behaviors) behavior within 2 meters of proximity and directed either at each other, or one individual directing affiliative behavior at a target. Only interventions into affiliative dyads previously recorded were counted. All event sampling (Altman, 1974) was used to record individual behavior during interventions into affiliative dyads (see appendix A). An intervention was defined as an agonistic, interposition, or pestering behavior pattern performed by a third individual and directed at one or both participants engaged in an affiliative dyad. A separating intervention was defined as the termination of the affiliative dyad at which the intervening individual (hereafter 'intervenor') directed intervention behaviors within 30 seconds of the onset of behaviors. Termination of an affiliative dyad was defined as one or both of the participants leaving proximity of the other. Upon termination of the affiliative dyad the intervenor was the subject of a ten minute focal follow where all social behaviors of the intervenor and targeted animal(s) were recorded.

Statistical Analyses

All statistical tests were 1-tailed. Non parametric chi-square X^2 tests were conducted using Excel version 11.2 for Mac OSX and Pearson rank correlations were conducted using MiniTab version 15.1.30 for Windows Vista.

Results

Rank Analysis

Tables 2 a-d present the results of the agonistic and displacement interactions used to determine rank. Rank was determined (when possible) by analyzing the direction and outcome of these interactions. Displacements were defined as individual A approaching individual B, where B leaves proximity of A not before A reaches <2 m proximity to B and where A sits in the place of or passes through the point occupied by B.

Distribution of Affiliative Dyads

A total of 586 affiliative dyads was recorded during the study resulting in a frequency of 2.483 (586/236) per observational hour (see Table 3). 131 of the dyads were individuals engaged in play behavior, 117 were grooming dyads, 54 were dyads of individuals engaged in socio-sexual behavior, 20 were the total copulations recorded, and 264 dyads were labeled as 'other' and included behaviors occurring with <1 m between participants and lasting over 1

minute such as embracing, touching (non-grooming), and sleeping in proximity (see Table 4 and Appendix A).

Of the 586 total recorded affiliative dyads, 225 were female-female dyads, 290 were male-female dyads, and 71 were male-male dyads (see Tables 5 a-c). Because all adult females had sub-adult offspring in the group, dyads without sub-adults were also calculated. Removing sub-adults from consideration yielded: 40 female-female dyads, 92 male-female dyads, and 15 male-male dyads (see Tables 5 e, g, and h). Additionally, two adult females had adult sons in the group and association patterns were also calculated without the mother-son dyads and resulted in: 82 adult male-adult female dyads (see Table 5 f).

The overall association pattern between all individuals was different than what would be expected at chance ($p<0.001$). Male-male dyads occurred significantly less than expected ($p<0.01$), female-female dyads occurred significantly more than expected ($p<0.01$), and male-female dyads occurred at expected levels of chance (analysis excluded mother-son dyads).

Males were involved in 61.60% (361/586) of the total recorded affiliative dyads. 80.33% (290/361) of these dyads involved a female and 19.67% (71/361) involved another male. Thus, males were engaged in dyads with females significantly more than with males ($p<0.001$).

Distribution of Affiliative Dyads by Individual Male Rank

The alpha male, D, was involved in the most affiliative dyads with total females, 21.03% (61/290), as well as with only adult females, 39.13% (36/92). The beta male, R, was next with 28.26% (26/92) of the total adult male – adult female dyads, followed by the fourth ranked male, J, with 18.48% (17/92), then the third ranked male, M, with 8.70% (8/92) and finally the lowest

rank male, T, with 5.43% (5/92). Because both the alpha, D, and beta, R, males had mothers in the group, association patterns were also calculated without mother-son dyads and resulted in: 35.37% (29/82) of the total for D and 28.05% (23/82) for R (see Tables 5 a, e, and f).

A correlation between adult male rank and adult female association approached significance with a Pearson's correlation value of 0.850 ($p = 0.068$). With mother-son dyads included in the analysis, the correlation was stronger but still non-significant (Pearson's value of 0.876 and $p = .052$). Adult male rank was significantly positively correlated with female association when all females were included (Pearson's value of 0.882 and $p = 0.048$).

Adult Male Mating Frequency and Rank

A total of 20 copulations were observed between males and adult females (see Table 5d). The two highest ranking males, D and R, and the two juvenile males, Ga and BI were observed copulating with an adult female at least once. The lowest rank adult males were never observed copulating with adult females. Although adult male rank was significantly and positively correlated with copulation frequency (Pearson's value of 0.891 and $p = 0.042$) (see Table 5i), the individual with the most copulations was BI (8/20 = 40.00%), a subordinate sub-adult male. Thus, male rank and copulation frequency were not significantly correlated.

Frequency and Distribution of Separated Affiliative Dyads

There were 94 separate occurrences of intervention behavior directed at affiliative dyads. 73 of these interventions were successful at terminating the dyad and were labeled as 'separating

interventions.' 21 were labeled as failed attempts to succeed resulting in an intervention success rate of 77.66% (73/94) (see Table 4).

Dyads containing an adult male had the highest proportion of all separated dyads at 68.49% (50/73). Dyads containing a juvenile female had a similar proportion of all separated dyads at 61.64% (45/73) and dyads containing a juvenile male had the next highest proportion of all separated dyads at 38.36% (28/73). Only one intervention into adult male – adult male dyads and no interventions into adult female – adult female or juvenile male – juvenile male dyads were observed (see Table 6).

Of the 50 separated dyads containing at least one adult male, the other participant was an adult female 20.00% (10/50) of the time and a juvenile female 60.00% (30/50) of the time (see Table 6). The proportion of total dyads separated was significantly skewed towards dyads containing an adult male and female participant ($p<0.001$).

Distribution of Separated Affiliative Dyads by Rank of Individual Adult Male Dyad Participant

The third ranked adult male was the only individual to ascend the dominance hierarchy. this individual, M, was involved in the highest proportion of separated dyads containing an adult male at 34.00% (17/50). Next was the second ranked male, R, at 26.00% (13/50), followed by the lowest rank male, T, at 22.00% (11/50), then the fourth ranked male, J, at 14.00% (7/50). The alpha male, D, was involved in the lowest proportion of separated dyads containing an adult male at 6.00% (3/50) (see Table 6). Although separations experienced by adult males showed a trend in rank increase and separations experienced, the results were not significant (Pearson's value of 0.604 and $p = 0.280$).

Distribution of Separated Affiliative Dyads by Individual Female Participant

The lowest ranking adult female, AN, was involved in the highest proportion of separated dyads containing an adult female at 70.00% (14/20), followed by the third rank female, L, at 20.00% (4/20), then the beta female, S, at 10.00% (2/20). The alpha female, U, was not involved in any separated dyads (see Table 6). A strong negative trend between female rank and separations experienced was observed but the results were not significant (Pearson's value of -0.914 and $p = 0.086$).

Distribution of Intervention Behavior Performed by Adult Males

Adult males performed the highest proportion of all separating interventions, accounting for 47.95% (35/73) of the total recorded. The highest proportion of these interventions were performed by the lowest ranked male, T, at 28.57% (10/35), followed by the fourth ranked male, J, at 25.71% (9/35), then the beta male, R, at 20.00% (7/35). Next was the alpha male, D, at 14.29% (5/35), and finally the third ranked male, M, at 11.43% (4/35) (see Table 7). Performance of intervention behavior was significantly and negatively correlated with male rank trajectory (Pearson's value of -0.881 and $p = 0.049$). Rank trajectory was defined as the absolute difference in the rank of an individual between the beginning and end of data collection.

The two lowest ranked males, J and T, each performed 100% of their respective total separating interventions, 9/9 and 10/10, into dyads containing the adult male M who ascended the dominance hierarchy during the course of the study, moving from the lowest rank position to

number 3, see Table 7. M began the study in the lowest adult male rank position (5) and ascended the hierarchy to position number 3 by the end of the study. J and T occupied adult male rank positions 3 and 4 at the beginning of the study and, after being displaced by M, ended the study at 4 and 5, respectively. Thus, M was both T and J's closest competitor and both T and J intervened into the dyad containing M significantly more than into any other dyad ($p<0.001$) (see Table 7).

Direction of High Rank Male Intervention Behavior

The two highest rank males, D and R, each performed 100% of their respective total separating interventions, 5/5 and 7/7, into dyads containing the two juvenile males, Ga (son of S) and BI (son of AN) (see Table 7). D and R both intervened into dyads containing either Ga or BI significantly more than any other dyad ($p<0.001$).

Age/Sex Class and Rank Effects Success Rate of Intervention Behavior

The overall success rate of all interventions into affiliative dyads was 77.66% (73/90) for the group and occurred significantly more than chance ($p<0.001$). Adult female success rate was 100% (11/11), adult male success rate was 83.33% (35/42), juvenile female success rate was 70.83% (17/24) and juvenile male success rate was 58.82% (10/17). All three adult females (S, L, and AN) that were observed performing interventions and the two highest ranking males (D and R) were 100% (6/6, 3/3, 2/2, 5/5, and 7,7 respectively) successful at performing separations. The two mid ranking males, J and M, had success rates of 81.82% (9/11) and 80.00% (4/5) (see

Table 4). Success rate of intervention behavior was significantly and positively correlated with individual (adult) rank (Pearson's value of 0.0858 and $p = 0.003$).

Discussion

Rank

In the current study population, a linear dominance hierarchy was determined for both male and female subjects, but the dominance hierarchy between males and females was less clear (see Table 2 d for the outcome of decided displacement and agonistic interactions). Two females outranked one male and the two lowest ranking adults were both male. The lowest ranking male at the onset of data collection was M. At that time both T and J were observed to be dominant to M based on agonistic and displacement interactions. The proceeding weeks yielded a shift in the outcome of agonistic interactions between M and T, and later between M and J. Some of the agonistic conflicts between M and J resulted in wounds to the extremities of J. By the end of the study period both T and J were observed performing submissive behaviors in response to the aggressive behaviors of M.

Bonobos have been labeled with virtually every possible dominance style applied to primates (Parish, 1996; Kano, 1996; Furuichi, 1997; Stanford, 1998; Boehm, 1999;). Nevertheless, dominance hierarchies have been reported in both wild and captive bonobo populations (Stevens et. al., 2007), confirming the existence of competition between individuals and suggesting that rank plays a role in maximizing fitness. Rank is particularly important to male bonobos and there is abundant evidence of the importance of rank to male reproductive

success, where high ranking males copulate more frequently and have greater paternity success than low rank males (Kano, 1996; Takahata et. al., 1996; Gerloff et. al., 1999; Vervaecke et. al., 2000; Hohmann and Fruth, 2003). Rank may be so important to male mating success that male bonobos fission and often travel with a small group of females unaccompanied by other males. By doing so, males increase their relative dominance rank, enabling them to engage in more frequent copulations with females than when in a larger party (Kano, 1996). During times of large party composition, male-female affiliation greatly increases (White, 1996) and males display differential access to the center of the group where females are highly cohesive. High ranking males and the sub-adult sons of high ranking females have access to the central area and subordinate males are forced to the periphery (Furuichi, 1997).

Chimpanzees (Boehm, 1999) are the consummate despotic species, where male dominance rank also strongly correlates with mating opportunities and male fitness, but where males are prevented from leaving their natal group because of the threat of fatal aggression from neighboring males. Additionally, all adult male chimpanzees dominate all females and utilize coercive mating as a reproductive strategy (Wrangham, 2002; Gilby and Wrangham, 2008). Therefore, the results presented in this paper support the hypothesis that rank in adult male bonobos has retained the same kind of differential effect as in chimpanzees and that male bonobos compete for higher dominance status.

Association Patterns

This study population showed a pattern of relationships similar to those observed in wild populations where female-female associations occurred significantly more than expected by

chance, male-female occurred at chance levels and male-male occurred significantly less than expected by chance. Males also significantly and preferentially chose females over other males for close association, lending evidence to the hypothesis that male relationships with females are more valuable than with other males (Hohmann, 2003). Although some of the distribution in wild populations can be explained in terms of mother-son association patterns, data from the current study show a significant and positive correlation between male rank and female association with mother-son dyads excluded.

Close inter-sexual association has consistently been observed in wild bonobo populations (White, 1996; Hohmann et. al., 1999; Hohmann and Fruth, 2003) even though the importance of female-female relationships has long been the hallmark of bonobo sociality (Parish, 1996). Although some of the distribution in frequencies of association in wild populations can be explained in terms of mother-son association patterns, data from this study support the notion that males also seek associations with unrelated females. Furthermore, males engage females as coalition partners in a manner similar to how male chimpanzees utilize other males for coalitionary rank gain (Hohmann et. al., 1999). Because female bonobos can dominate males, it pays for male bonobos to invest in relationships with females and to cultivate them as coalition partners in their rank efforts.

Social bonds in primates can be considered a product of the investments individuals choose to cultivate in order to maximize their fitness (Watts, 2002). In chimpanzees, male-male associations are the most prevalent type of social relationship, probably reflecting the relative importance of the intra-sexual bond to male fitness. Males cooperate to increase reproductive success by forming coalitions to monopolize females, to increase rank, and to defend and expand the group's territory. Males maintain and compete for these cooperative bonds by engaging in

affiliative dyads such as grooming (Watts, 2002). In chimpanzees, grooming bouts between males are longer than both male-female and female-female bouts (Muroyama et. al., 1994). Additionally, grooming bouts between close male associates are longer than between non-associates (Watts, 2002) and rival males perform separating interventions into these dyads to prevent the formation of close associations (deWaal, 1982). In sum, chimpanzee males form close bonds with each other and cooperate to monopolize females. Bonobo males, in contrast, cultivate male-female relationships most likely to maximize mating success. The difference in preferred association partners between male chimpanzees and bonobos likely reflects differences in the strategies males utilize to maximize fitness.

Distribution of Separating Intervention Behavior

This paper examines the distribution and direction of a political maneuvering behavior termed 'separating interventions' in a captive group of bonobos. The goal of this study was to advance our understanding of the bonobo social system by testing hypotheses concerning the significance of inter-sexual social bonds to male fitness and to identify close male competitors and the political behavior of rivals. The delineation of separating intervention behavior can help determine the relative importance of intra- and inter-sexual relationships to different individuals. The results of this recorded behavior are broken down into two categories for further discussion.

1. Interventions Experienced

Because of the prevalence of male-female relationships and the importance of inter-sexual association to male reproductive success, relationships between adult males and females are highly valuable and I suggested that this would be reflected in the distribution of separated affiliative dyads. The data presented in this paper support this notion by showing a significant skew towards adult male-female dyads relative to all separated dyads recorded. In contrast to the data on chimpanzees (deWaal, 1982), only a single intervention into an adult male-adult male dyad was observed and no interventions into adult female-adult female dyads were observed. These results further support the hypothesis that salient male-male relationship ubiquitous among chimpanzees has been replaced with a male-female counterpart in bonobos.

Although rank trajectory did not significantly correlate with affiliative dyad separations experienced, the adult male involved in the most frequently separated dyads was M, the only individual that ascended the dominance hierarchy during the course of the study. Interestingly, the majority of separations experienced by adult males, and M in particular, were into dyads with juvenile females. There are three wild behavioral patterns that help provide a plausible explanation. First, it has been suggested that adult male bonobos show attractivity to nulliparous females primarily because, as female bonobos immigrate into new populations, they show continual estrous and proceptivity as a means to establish necessary social bonds (Wrangham, 2002). Further, it has been reported that nulliparous female bonobos copulate more frequently than both bonobo and chimpanzee adult females (Takahata et. al., 1996). Secondly, the adult male M primarily associated with the daughter, Lo, of the previous alpha female, S. While female immigration has been confirmed in bonobos, both males and females disappear from the

group at the same frequency (Gerloff et. al., 1999) and in chimpanzee populations such as those at Bossou and Gombe, females often stay in their natal community, particularly if their mothers are high rank (Stanford, 1998; Parish, 1996). By creating bonds with a sub-adult female, M could be establishing a relationship for future coalitionary use. Third, M was originally the lowest rank male and his pattern of intersexual association was reflected in his status. Although captive, M spent the majority of his time on the 'periphery,' particularly in the beginning of the study, and thus associated more with lower rank individuals such as sub-adult females.

The absence of separating interventions into adult female-adult female dyads suggests that females do not compete for intra-sexual bonds and that males are not competitive with other females for inter-sexual bonds. This behavioral pattern fits predictions about the difference in the salient resources utilized by the sexes, where females compete with other females for nutritional resources and males compete with other males for access to females (Trivers, 1972).

Additionally, the separations experienced by females engaged in other age/sex class dyads showed a strong and negative relationship with rank order, where the alpha female experienced no separations while engaged in affiliative dyads. One possible explanation may be related to the aggressive nature of the behavior. Observed intervention behavior ranged from mild pestering to aggression resulting in agonistic conflicts. Because females occupied positions of high rank, it is possible that females would object to intervention behavior from low rankers, including competing males, which could result in an aggressive confrontation. Vervaecke et. al. (2000) reported that in captivity, male bonobos did not interfere in the copulations of females because females occupied the two highest rank positions. Kano (1996) describes this behavior as a kind of female choice, where males are prevented from monopolizing females in the presence of other males because the female may be dominant to the male. Also, threat of retaliation from

female-female coalitions may be increased in captivity (White, 2007) and could possibly act as a deterrent. Male reluctance to interfere in the dyads of adult females may also be related to the male strategy of forming close associations with females. Hohmann and Fruth (2003) reported that males never aggressed their close female associates and that copulation frequency was greater between close male-female associates than non-associates.

2. Interventions Performed

I predicted that the distribution of separating intervention behavior performed by males resulted from male-male competition and would be directed at affiliative male-female dyads. The current study found that adult males performed significantly more interventions than any other age/sex class into these inter-sexual dyads. This result supports the hypothesis that male bonobos are utilizing a political strategy of disturbing the reproductively salient male-female bonds of rivals.

I further predicted that adult males would direct this competitive maneuver at their closest rivals and found support for this argument by examining the intervention behavior of individual adult males. Interventions performed by adult males into male-female dyads were significantly and negatively correlated with male rank trajectory. The two males that performed most interventions were T and J, two individuals who descended the dominance hierarchy during the course of the study. Both males significantly directed their behavior at their closest rank competitor, M, the individual that surpassed them on the dominance hierarchy. It was apparent that both T and J lost their rank via agonistic conflicts with M and because they were not able to win direct contests with this rival, it is reasonable that they utilized separating interventions as an

alternate competitive strategy. It remains to be seen whether this behavior was continued and if it resulted in a turnaround of the observed rank changes.

Interestingly, in the present study, the two highest ranking males, D and R, significantly directed their intervention behavior at the two sub-adult males, Ga and BI. These four males, (D, R, Ga, and BI) were the only males with mothers (S, L, U, and AN respectively) present in the group *and* were the only males that engaged in copulations. This is important not only because of the reported correlation between male rank and the presence of mothers (Furuichi, 1997), but field data that suggests male bonobos can reach a peak in copulation frequency at an earlier age than chimpanzees. Young mothers that give birth to sons reach their physical prime when their offspring are still sub-adult, suggesting that the mother's age can impact the age at which males reach their reproductive prime (Furuichi, 1997). The mothers of D and R were much older than the mothers of the sub-adult males, Ga and BI. Thus, it is possible that Ga and BI were the closest rivals to D and R and that D and R employed separating interventions to both disrupt the bonds of close rivals and to maintain dominance status. Further, these results suggest that the greatest competitors to high ranking males can be sub-adult males with mothers in their physical prime.

Evidence from both *Pan* species, show that the highest ranking males garner the most copulations and in chimpanzees, dominant males gain this advantage partly by intervening into the copulations of subordinates (Wrangham, 2002). Similar results were reported in bonobos, where adult males intervene into the copulations of adolescent males with parous females (Wrangham, 2002) and Hohmann et. al. (2003) reported that low rank male matings were often disturbed.

Summary

There are two types of relationships that are most frequently discussed in the literature on bonobo sociality. First and most widely discussed is the intra-sexual female bond. The function of this relationship is largely thought to be a mechanism by which females monopolize food patches. Females also use these relationships, albeit most likely in captivity, as a mechanism for dominating males. The second type of abundant association is the male-female relationship. While the occurrence of long lasting bonds between bonobo mothers and sons exist, there is mounting evidence that unrelated males and females form close associations and that these associations are beneficial to males. Some argue that this type of relationship is a byproduct of mother-son association patterns but, regardless of origin, it is becoming clear that males are competing for these reproductively valuable bonds. Coupled with high rank status, male-female associations may be the most important factor concerning male reproductive success. This contrasts with chimpanzees, where close association with females has a negligible impact on mating success and males form close intra-sexual bonds and coalitions to maximize fitness.

Political maneuvers such as coalitions occur in both *Pan* species and separating interventions are an important mechanism that can shed light on the nature of social systems in species capable of multiple mating strategies. The present study found a differential distribution of both type of dyad separated, as well as performance of separating behaviors. The results presented strongly suggest that separating interventions are employed, primarily by adult males, as a counter-strategy to the establishment of their closest rivals' inter-sexual bonds, and, as an alternate mechanism to agonistic conflicts in the establishment of a dominance hierarchy. Because female bonobos often intervene into male contests (Boose and Kitchen, in prep), males

can potentially circumvent direct competition by employing separating intervention behavior. Additionally, because bonobos exhibit less frequent and less intense aggression relative to chimpanzees, evidence of this alternate political mechanism may be the result of a reduction in the efficacy of male aggression in a non-patriarchic social system.

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Tables

Table 1. Pan paniscus *colony at the Columbus Zoo and Aquarium*

Subject	Sex	Class	Date of birth	Offspring of:	Adult Rank[5]
U (Unga)	F	Adult	1993 captivity		1
S (Susie)	F	Adult	1982[1] wild		2
D (Donnie)	M	Adult	1993 captivity	Susie and Jimmy	3
L (Lady)	F	Adult	1982[1] wild		3
AN (Ana Neema)[3]	F	Adult	1992 captivity		4
R (Ricky)	M	Adult	1995 captivity	Lady and Jimmy	4
M (Maiko)	M	Adult	1984 captivity		5
J (Jimmy)	M	Adult	1979[1] wild		6
T (Toby)	M	Adult	1979[1] wild		7
Ga (Gander)	M	Juvenile	2003 captivity	Unga and Mambo[2]	-
JT (Jo-T)	F	Juvenile	2002 captivity	Lady and Mambo[2]	-
Lo (Lola)	F	Juvenile	2004 captivity	Susie and Toby	-
BI (Bila-Isia)[3]	M	Juvenile	2001 captivity	Ana Neema	-
Gi (Gilda)[3]	F	Infant	2006 captivity	Ana Neema	-
Je (Jerry)[4]	M	Infant	2009 captivity	Unga and Donnie	-

[1]*estimated age*

[2]*deceased before start of the study*

[3]*arrived at CZA during onset of the study*

[4]*born during the course of the study and not included in the data*

[5]*see results for discussion*

Table 2a. Matrix of total observed agonistic dyads by individual and rank

	Recipient														
Actor	U	S	D	L	R	M	J	T	AN	JT	Lo	Ga	BI	Gi	Total
U	/	-	-	-	2	1	-	-	-	-	-	-	3	-	6
S	-	/	-	-	1	-	-	-	-	-	-	-	-	-	1
D	-	-	/	-	-	-	-	-	-	-	-	-	1	-	1
L	-	-	-	/	-	-	-	-	-	-	1	-	-	-	1
R	-	-	-	-	/	2	-	1	-	-	-	2	-	-	5
M	-	-	-	-	-	/	6	4	-	-	-	-	-	-	10
J	-	-	-	-	-	2	/	-	-	-	-	-	-	-	2
T	-	-	-	-	-	1	-	/	-	-	-	-	-	-	1
AN	-	-	-	-	-	-	-	-	/	-	-	-	-	-	-
JoT	-	-	-	-	-	-	-	-	-	/	2	2	1	1	6
Lo	-	-	-	-	-	-	1	-	-	2	/	-	-	2	5
Ga	-	-	-	-	1	2	-	-	-	1	-	/	-	-	4
BI	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gi	-	-	1	-	1	-	-	-	-	-	1	-	1	/	4
Total	-	-	1	-	5	8	7	5	-	3	4	4	6	3	46

Table 2b. Matrix of decided agonistic interactions by individual and rank

	Recipient														
Actor	U	S	D	L	R	M	J	T	AN	JT	Lo	Ga	BI	Gi	Total
U	/	-	-	-	2	1	-	-	-	-	-	-	3	-	6
S	-	/	-	-	1	-	-	-	-	-	-	-	-	-	1
D	-	-	/	-	-	-	-	-	-	-	-	-	1	-	1
L	-	-	-	/	-	-	-	-	-	-	1	-	-	-	1
R	-	-	-	-	/	2	-	1	-	-	-	2	-	-	5
M	-	-	-	-	-	/	6	4	-	-	-	-	-	-	10
J	-	-	-	-	-	2	/	-	-	-	-	-	-	-	2
T	-	-	-	-	-	1	-	/	-	-	-	-	-	-	1
AN	-	-	-	-	-	-	-	-	/	-	-	-	-	-	-
JoT	-	-	-	-	-	-	-	-	-	/	-	-	1	1	2
Lo	-	-	-	-	-	-	-	-	-	-	/	-	-	2	2
Ga	-	-	-	-	-	-	-	-	-	-	-	/	-	-	-
BI	-	-	-	-	-	-	-	-	-	-	-	-	/	-	-
Gi	-	-	-	-	-	-	-	-	-	-	-	-	-	/	-
Total	-	-	-	-	3	6	6	5	-	-	1	2	5	3	31

Table 2c. Matrix of decided displacement interactions by individual and rank

	Recipient														
Actor	U	S	D	L	AN	R	M	J	T	Ga	JT	Lo	BI	Gi	Total
U	/	2	-	-	2	-	2	1	-	1	-	-	2	-	10
S	-	/	1	-	1	-	-	-	-	-	1	-	-	-	3
D	-	-	/	1	2	3	-	-	-	2	1	1	6	-	16
L	-	-	-	/	-	1	2	-	1	-	-	-	-	-	4
AN	-	-	-	-	/	1		1	-	-	1	-	-	-	3
R	-	-	-	-	-	/	2	2	-	-	1	-	2	-	7
M	-	-	-	-	-	1	/	1	-	-	-	-	-	-	2
J	-	-	-	1	-	-	1	/	1	-	-	-	-	-	3
T	-	-	-	-	-	-	-	-	/	-	-	-	-	-	-
Ga	-	-	-	-	-	1		1	-	/	1	-	-	-	3
JoT	-	-	-	-	-	-	1		-	-	/	-	-	-	1
Lo	-	-	-	-	-	-	-	1	-	-	-	/	-	-	1
BI	-	-	-	-	-	-	-	-	-	-	1	-	/	-	1
Gi	-	-	-	-	-	-	-	-	-	-	-	-	-	/	-
Total	-	2	1	2	5	7	8	7	2	3	6	1	10	-	53

Table 2d. Matrix of decided agonistic and displacement interactions by individual and rank

	Recipient														
Actor	U	S	D	L	AN	R	M	J	T	Ga	JT	Lo	BI	Gi	Total
U	/	2	-	-	2	2	3	1	-	1	-	-	5	-	16
S	-	/	1	-	1	1	-	-	-	-	1	-	-	-	4
D	-	-	/	1	2	3	-	-	-	2	1	1	7	-	17
L	-	-	-	/	-	1	2	-	1	-	-	1	-	-	5
AN	-	-	-	-	/	1	-	1	-	-	1	-	-	-	3
R	-	-	-	-	-	/	4	2	2	1	1	-	2	-	12
M	-	-	-	-	-	1	/	7	4	-	-	-	-	-	12
J	-	-	-	1	-	-	3	/	1	-	-	-	-	-	5
T	-	-	-	-	-	-	1	-	/	-	-	-	-	-	1
Ga	-	-	-	-	-	1	-	1	-	/	1	-	-	-	3
JoT	-	-	-	-	-	-	1	-	-	-	/	-	1	1	3
Lo	-	-	-	-	-	-	-	1	-	-	-	/	-	2	3
BI	-	-	-	-	-	-	-	-	-	-	1	-	/	-	1
Gi	-	-	-	-	-	-	-	-	-	-	-	-	-	/	-
Total	-	2	1	2	5	10	14	13	8	4	6	2	15	3	85

Table 3. Matrix of total affiliative dyads from focal samples

	U	S	L	AN	D	R	M	J	T	JT	Lo	Gi	Ga	BI	Total
U	/	-	3	5	6	9	2	7	3	3	3	2	12	1	56
S	-	/	11	10	7	5	3	8	-	10	23	5	1	7	90
L	3	11	/	11	6	3	3	-	-	21	2	12	5	11	88
AN	5	10	11	/	17	9	-	2	2	19	12	26	10	4	127
D	6	7	6	17	/	3	-	-	1	6	4	15	2	12	79
R	9	5	3	9	3	/	-	4	1	5	2	3	8	6	58
M	2	3	3	-	-	-	/	3	2	8	16	-	2	1	40
J	7	8	-	2	-	4	3	/	1	8	8	3	3	7	54
T	3	-	-	2	1	1	2	1	/	6	5	-	1	7	29
JT	3	10	21	19	6	5	8	8	6	/	14	13	8	13	134
Lo	3	23	2	12	4	2	16	8	5	14	/	20	9	9	127
Gi	2	5	12	26	15	3	-	3	-	13	20	/	12	7	118
Ga	12	1	5	10	2	8	2	3	1	8	9	12	/	7	80
BI	1	7	11	4	12	6	1	7	7	13	9	7	7	/	92
															1172

Table 4. Separated Affiliative Dyad Behavior by Individual and Age/Sex Class of Intervenor

	Dyad Behavior						
Intervenor	Socio-Sex	Play	Grooming	Copulation	Proximity	Total[1]	% Success
Adult Males							
D	-	3	2	-	-	5(5)	100.00%
R	3	3	1	-	-	7(7)	100.00%
M	3	-	1	-	-	4(5)	80.00%
J	5	4	-	-	-	9(11)	81.82%
T	5	5	-	-	-	10(14)	71.43%
Total						**35(42)**	83.33%
Adult Females							
U	-	-	-	-	-	-	-
S	2	3	1	-	-	6(6)	100.00%
L	-	1	1	1	-	3(3)	100.00%
AN	-	1	1	-	-	2(2)	100.00%
Total						**11(11)**	100.00%
Juv. Females							
JT	-	3	-	-	-	3(4)	75.00%
Lo	-	-	1	-	-	1(3)	33.33%
Gi	6	-	3	4	-	13(17)	76.47%
Total						**17(24)**	70.83%
Juv. Male							
Ga	1	-	-	4	3	8(12)	66.67%
BI	-	1	-	1	-	2(5)	40.00%
Total	25	24	11	10	3	**10(17)**	58.82%
TOTAL						**73(94)**	77.66%

[1]*(N) = attempts*

Table 5 a-i. Matrices of affiliative dyads: a) Male/Female b) Female-Female c) Male-Male d) Copulations e) Male/Female Without Juveniles f) Male/Female Without Juveniles or Mother/Son Dyads g) Male/Male Without Juveniles h) Female/Female Without Juveniles i). Copulations Without Juveniles

a.

	Males							
Fem.	D	R	M	J	T	Ga	BI	
U	6	9	2	7	3	12	1	
S	7	5	3	8	-	1	7	
L	6	3	3	-	-	5	11	
AN	17	9	-	2	2	10	4	
JT	6	5	8	8	6	8	13	
Lo	4	2	16	8	5	9	9	
Gi	15	3	-	3	-	12	7	
	61	36	32	36	16	57	52	290

b.

	Females							
Fem.	U	S	L	AN	JT	Lo	Gi	
U	/	-	-	-	-	-	-	
S	-	/	-	-	-	-	-	
L	3	11	/	-	-	-	-	
AN	5	10	11	/	-	-	-	
JT	3	10	21	19	/	-	-	
Lo	3	23	2	12	14	/	-	
Gi	2	5	12	26	13	20	/	
	16	59	46	57	27	20	0	225

c.

	Males							
Males	D	R	M	J	T	Ga	BI	
D	/	-	-	-	-	-	-	
R	3	/	-	-	-	-	-	
M	-	-	/	-	-	-	-	
J	-	4	3	/	-	-	-	
T	1	1	2	1	/	-	-	
Ga	2	8	2	3	1	/	-	
BI	12	6	1	7	7	7	/	
	18	19	8	11	8	7	0	71

Copulation:

d.

	Males							
Fe.	D	R	M	J	T	Ga	BI	
U	1	-	-	-	-	-	-	
S	-	-	-	-	-	-	-	
L	-	-	-	-	-	-	8	
AN	6	4	-	-	-	1	-	
	7	4	-	-	-	1	8	20

e.

	Males					
Fem.	D	R	M	J	T	
U	6	9	2	7	3	
S	7	5	3	8	-	
L	6	3	3	-	-	
AN	17	9	-	2	2	
	36	26	8	17	5	92

f.

	Males					
Fem.	D	R	M	J	T	
U	6	9	2	7	3	
S	-	5	3	8	-	
L	6	-	3	-	-	
AN	17	9	-	2	2	
	29	23	8	17	5	82

g.

Males	Males D	R	M	J	T	
D	/	-	-	-	-	
R	3	/	-	-	-	
M	-	-	/	-	-	
J	-	4	3	/	-	
T	1	1	2	1	/	
	4	5	5	1	0	15

h.

Fem.	Females U	S	L	AN	
U	/	-	-	-	
S	-	/	-	-	
L	3	11	/	-	
AN	5	10	11	/	
	8	21	11	0	40

Copulation:

i.

Fe.	Males D	R	M	J	T	
U	1	-	-	-	-	
S	-	-	-	-	-	
L	-	-	-	-	-	
AN	6	4	-	-	-	
	7	4	-	-	-	11

Table 6. Distribution of Separated Affiliative Dyads by Individual and Age/Sex Class

	Adult Males					Adult Females				Juv. Females			Juv. Males		
	D	R	M	J	T	U	S	L	AN	JT	Lo	Gi	Ga	BI	Total
D	/	-	-	-	-	-	-	-	2	-	1	-	-	-	3
R	-	/	-	-	-	-	1	-	6	1	1	-	-	4	13
M	-	-	/	-	1	-	-	1	-	3	12	-	-	-	17
J	-	-	-	/	-	-	-	-	-	2	5	-	-	-	7
T	-	-	1	-	/	-	-	-	-	2	3	-	-	5	11
U	-	-	-	-	-	/	-	-	-	-	-	-	-	-	-
S	-	1	-	-	-	-	/	-	-	-	-	-	-	1	2
L	-	-	1	-	-	-	-	/	-	1	-	-	-	2	4
AN	2	6	-	-	-	-	-	-	/	1	-	-	5	-	14
JT	-	1	3	2	2	-	-	1	1	/	-	-	3	1	14
Lo	1	1	12	5	3	-	-	-	-	-	/	2	-	1	25
Gi	-	-	-	-	-	-	-	-	-	-	2	/	4	2	8
Ga	-	-	-	-	-	-	-	-	5	3	-	4	/	-	12
BI	-	4	-	-	5	-	1	2		1	1	2	-	/	16
Total	3	13	17	7	11	-	2	4	14	14	25	8	12	16	
Correcting for					**51**				**20**			**47**		**28**	**146**
					(1)				*(0)*			*(2)*		*(0)*	
same age/sex class					*AM+AM=**50***				*AF+AF=**20***			*JF+JF=**45***		*JM+JM=**28***	***143***

Table 7. Type of Separated Affiliative Dyad by Individual and Age/Sex Class of Intervenor

	Type of Affiliative Dyad Separated										
Intervenor	AM/JF	JF/JM	AM/AF	AM/JM	AF/JM	JF/JF	AF/JF	AM/AM	AF/AF	JM/JM	TOTAL
Adult Males											
D	-	3	-	-	2	-	-	-	-	-	5
R	-	5	-	-	2	-	-	-	-	-	7
M	4	-	-	-	-	-	-	-	-	-	4
J	9	-	-	-	-	-	-	-	-	-	9
T	10	-	-	-	-	-	-	-	-	-	10
Total											**35**
Adult Females											
U	-	-	-	-	-	-	-	-	-	-	-
S	2	2	2	-	-	-	-	-	-	-	6
L	-	1	-	-	-	1	-	1	-	-	3
AN	-	-	-	1	-	1	-	-	-	-	2
Total											**11**
Juvenile Females											
JT	3	-	-	-	-	-	-	-	-	-	3
Lo	-	-	-	-	-	-	1	-	-	-	1
Gi	-	-	4	5	4	-	-	-	-	-	13
Total											**17**
Juvenile Males											
Ga	1	-	4	3	-	-	-	-	-	-	8
BI	1	-	-	-	-	-	1	-	-	-	2
Total											**10**
TOTAL	30	11	10	9	8	2	2	1	-	-	**73**

***Appendix A**: List of Behaviors*

I. Aggressive Behaviors (see Kano, 1992)

1. Chasing – tensed running toward another individual over a long distance, no shorter than 5 meters.
2. Charging – tensed running toward another individual over a short distance, no longer than 5 meters.
3. Physical Contact Aggression – intentional hitting, kicking, slapping, dragging, pulling, pushing or biting of a body part of another individual.
4. Threaten – tensed gesticulating or very short (less than 3 meters) charge behavior directed at an individual.
5. Swinging at target – intentional movement (of body or object) past an individual resulting in brief physical contact.
6. Display behavior – tensed running or pushing of an object in the direction of, parallel to, or past another individual.

- Pilo-erection usually occurred during all aggressive behaviors.

II. Affiliative Behaviors

1. Sociosexual Behavior – all non-copulatory genital-genital contact between individuals.
2. Copulation – intromission of an individual male's penis into the vagina of a female, usually accompanied by thrusting movements.
3. Play – prolonged pattern of affiliative touching resulting in the appearance of a 'play face' on individual participants.
4. Grooming – prolonged pattern touching where one individual runs their fingers and mouth over the hair and skin of another individual, sometimes removing excess skin and debris.
5. Touching, not agonistically – where an individual is sitting or laying in direct physical contact of another individual and/or where an individual is touching (not grooming) another individual with their hands or feet.
6. Embracing – where individuals press their torsos together (ventro-ventral or dorso-ventral) and wrap their arms and/or legs around the body of the other individual.
7. Proximity (affiliative) – where individuals are <1 m apart for >1 minute. [Standard proximity was measured as individuals less than 2 meters apart.]

III. Intervention Behaviors

1. Interposition behavior– where a third individual places themselves in between two individuals engaged in an affiliative dyad.
2. Pestering behavior – where an individual performs a repeated mild aggressive behavior pattern directed at one or both dyad participants.
3. Display behavior (see above) – directed at one or both dyad participants.
4. Agonistic behavior (see above) – directed at one or both dyad participants.

IV. Submissive Behaviors (see Kano, 1992)

1. Crouching –bowing or lowering of body posture by an individual in response to the aggressive behavior (see above) of another individual, usually accompanied by teeth-baring.
2. Screaming – prolonged vocal expulsions by an individual in response to the aggressive behavior (see above) of another individual, usually accompanied by fleeing.
3. Teeth-baring – exposure of the upper row of teeth by an individual in response to the aggressive behavior (see above) of another individual.
4. Fleeing – tensed running by an individual in response to and away from the aggressive behavior (see above) of another individual.
5. Avoiding – tensed walking away from and/or circumvention around another individual.